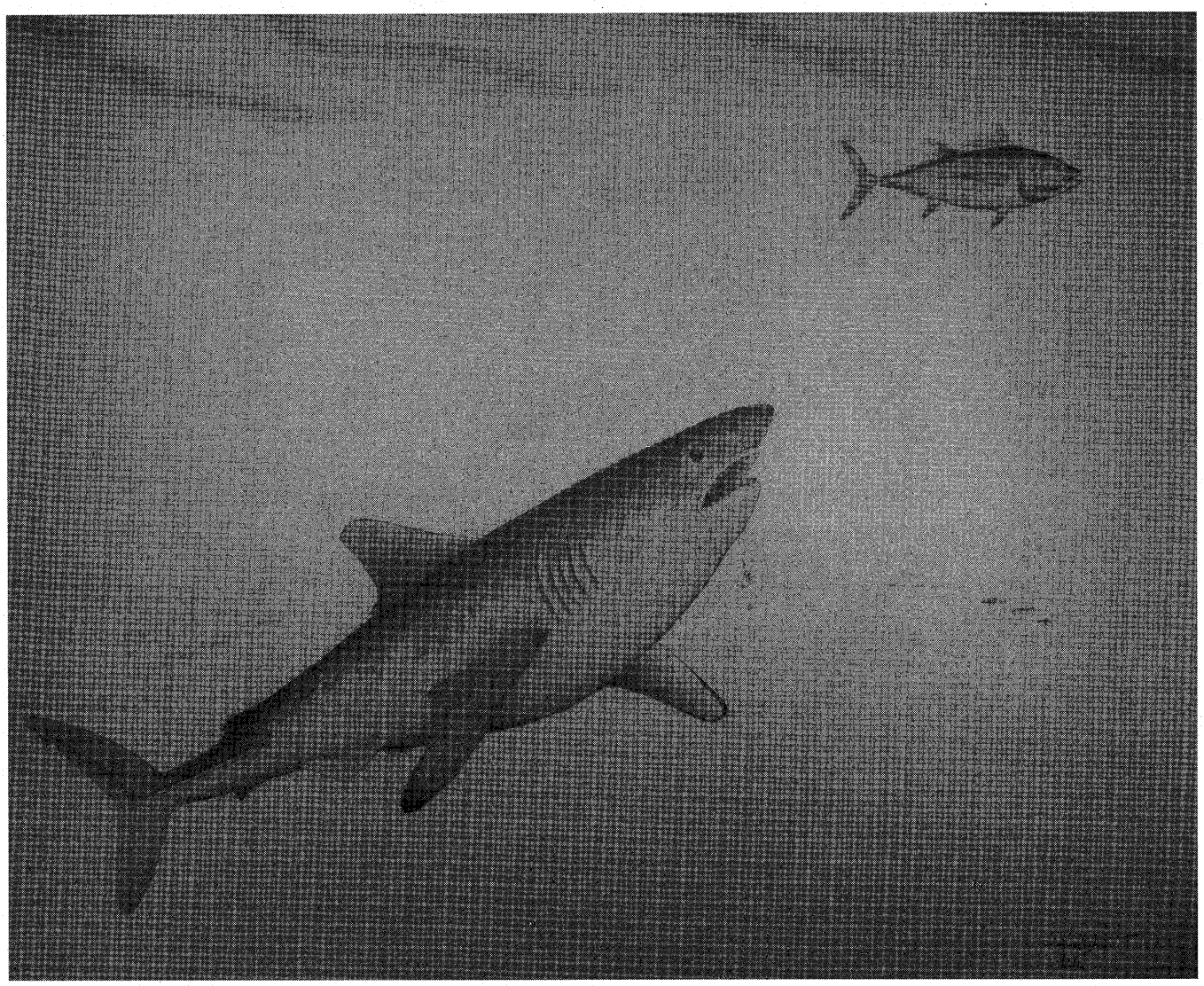
THE MOSASAUR



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COVER ART– "*Parotodus* Stalking Tuna" by David J. Kent.

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Contents

Reconstructed Dentition of the Rare Lamnoid Shark *Parotodus benedeni* (le Hon) from the Yorktown Formation (Early Pliocene) at Lee Creek Mine, North Carolina
BRETTON W. KENT AND GEORGE W. POWELL, JR 1

Speculations on the Size and Morphology of the Extinct Lamnoid Shark, *Parotodus benedeni* (le Hon)
BRETTON W. KENT 11

A Late Cretaceous (Severn Formation) Vertebrate Assemblage from Bowie, Maryland
EUGENE F. HARTSTEIN, LAWRENCE E. DECINA AND RONALD F. KEIL 17

Cretolamna cf. *C. aschersoni* (Stromer) (Neoselachii: Cretoxyrhinidae), from the Late Paleocene/Early Eocene of Mississippi, USA, with Comparisons to Moroccan Fauna
GERARD R. CASE AND JAMES J. LEGGETT 25

Upper Cretaceous Macroinvertebrate Faunas of the Northern Atlantic Coastal Plain
DANIEL F. KUEHNE 29

A Pleistocene Mollusk Assemblage from Cooper River, New Jersey
STEPHEN KURTH AND ERIC KURTH 81

A Large Coelacanth, c.f. *Diplurus* (*Pariostegus*) *longicaudatus,* from the Late Triassic Lockatong Formation, Granton Quarry, North Bergen, New Jersey
CHARLES A. RIZZO 85

Evidence for Live Birth in the Triassic Coelacanth *Diplurus (Osteopleurus) newarki*
CHARLES A. RIZZO 91

The Parlin Pit: Paleontology, Stratigraphy, and Depositional Environments at a Cretaceous Amber Site in New Jersey
WILLIAM B. GALLAGHER, KIRK R. JOHNSON, EDWARD GILMORE AND RALPH JOHNSON 97

A Scene from American Deep Time: New York's Palaeozoic Museum – Revisited
ALLEN A. DEBUS AND STEVE MCCARTHY 105

Evidence for Live Birth in the Triassic Coelacanth *Diplurus (Osteopleurus) newarki*

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ABSTRACT — New specimens of the Triassic coelacanth *Diplurus (Osteopleurus) newarki* appear to preserve a female and offspring in the act of parturition, strengthening the argument for viviparity in fossil coelacanths. Reproductive evidence from the extinct coelacanths *Undina penicillata* and *Rhabdoderma exiguum* has been cited as consistent with fossil coelacanth viviparity. However, this evidence remains neither robust nor uncontroversial. The new specimens suggest that abundant *D. newarki* in museum collections represent a population sample which may allow further examination of the hypothesis that *Latimeria* - style viviparity is phylogenetically widespread in fossil coelacanths.

Introduction

Coelacanths have an extraordinarily long geological record. They have remained anatomically conservative from their first appearance in the Middle Devonian sediments to the extant genus *Latimeria* (Schaeffer, 1952; Thomson, 1991). *Latimeria* has been known to be viviparous since the report of Smith, et al. (1975) which also claims that all of the reproductive evidence from fossil coelacanths, isolated large yolk-sac larvae of the Middle Pennsylvanian species *Rhabdoderma exiguum* (Schultze, 1972) and a single example of preservation of two large internal embryos in a specimen of the Jurassic species *Undina (Holophagus) Penicillata* (Watson, 1927), is consistent with live birth in extinct coelacanths as well. The implicit hypothesis, that a *Latimeria* - like viviparity is phylogenetically widespread among fossil coelacanths, has become widely accepted on the basis of this evidence (see for example Thomson, 1991).

The finding that reproductive style in *Latimeria*, including extremely large eggs, a relatively small number of large, well developed young and viviparity, exemplifies a precocial reproductive habit traceable to at least the middle Pennsylvanian in coelacanths could have important implications for the extraordinary anatomical conservatism and extreme longevity of this group of fishes. Such a hypothesis requires a much more detailed examination than it has received. Additional data relating to fossil coelacanth reproduction is needed.

New specimens of the coelacanth *Diplurus (Osteopleurus) newarki* from the New Jersey Late Triassic Lockatong formation appear to represent a female and offspring in the act of parturition. A description of these specimens and comparison of evidence relating to reproduction from the specimens with previously reported data on reproduction from extant and extinct coelacanths form the basis of this report. The possibility that abundant *D. newarki* preserved in museum collections will allow further examination of the fossil coelacanth viviparity hypothesis is discussed.

Abbreviations

Morphology

An:	adult anal fin
Co:	conchostracan (cf. *Cyzicus* sp) fragment
D1:	adult first dorsal fin
D2:	adult second dorsal fin
Jca:	juvenile tri-lobed caudalis
Pel:	adult pelvic fin
Sc:	adult scales.

Institutions

NJSM: New Jersey State Museum.

Materials and Methods

NJSM 16697 - a 4 x 7 cm black shale float from the east face of Granton Quarry, North Bergen, NJ, USA. Part only (counterpart unknown) contains partial *D. newarki* specimens and associated conchostracans (cf. *Cyzicus* sp.). The source beds consist of gray to black shales, massive mudstones and sandstones which comprise the late Carnian Age Lockatong Formation lake bed strata at this Newark Basin site (Colbert, 1965; Olsen, 1980; Olsen and Flynn, 1989; Olsen, 1991).

Specimen preparation consisted of a water rinse with gentle brushing. Photographs of the specimens were obtained under oblique lighting conditions.

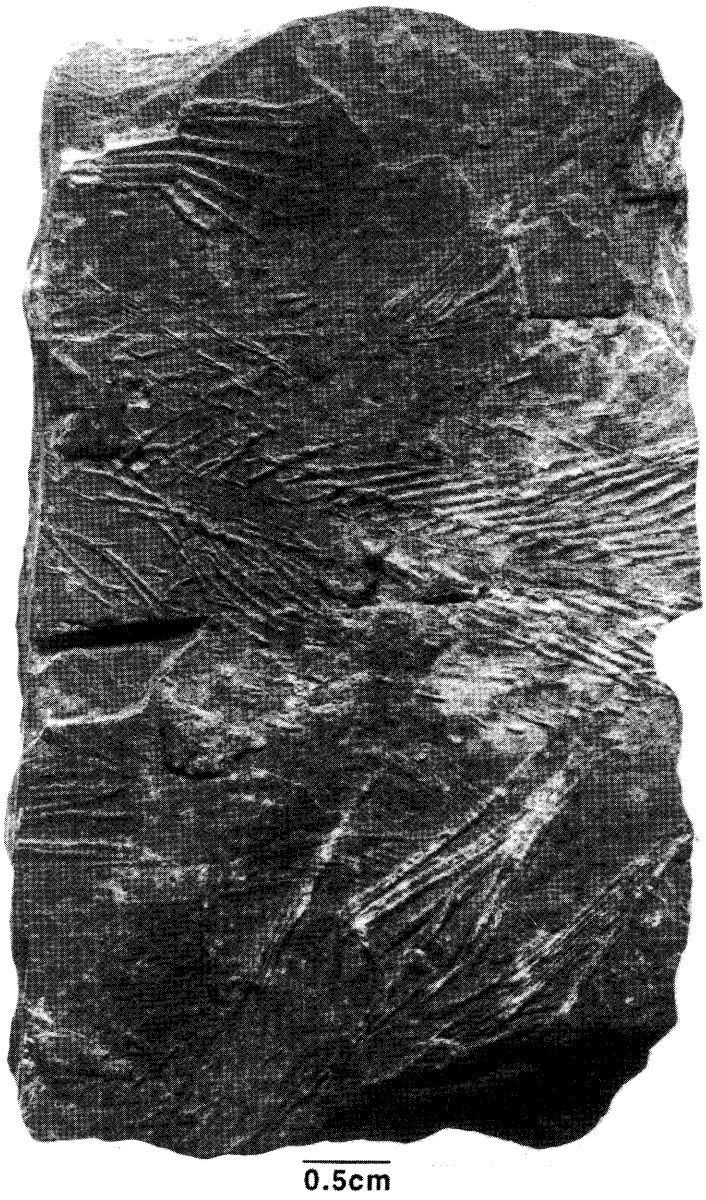
Total body length estimates for *D. newarki* individuals on NJSM 16697 were based on proportions of a skeletal reconstruction by Schaeffer (1952, fig. 9).

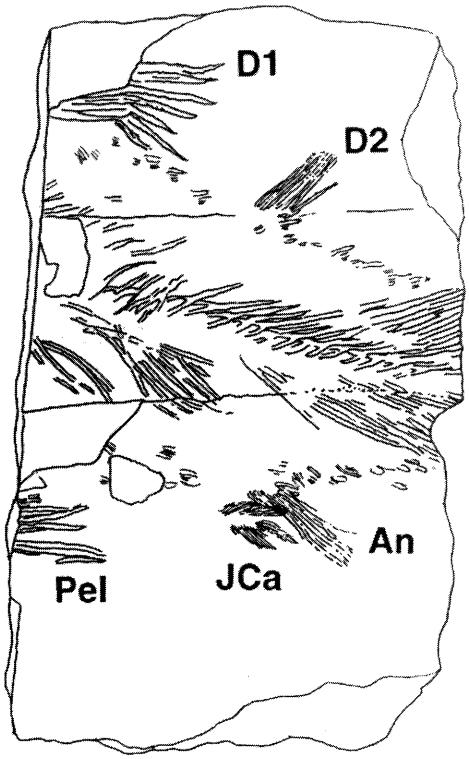
Description of NJSM 16697

NJSM 16697, illustrated in Figs. 1 and 2, contains the following. A 4 cm long articulated adult *D. newarki* midsection

including second dorsal and anal fins, distal portions of the first dorsal and pelvic fins, and an intact scale covering. It is recognized as *D. newarki* by species characteristics described in Schaeffer (1952) including: rough body length estimate of 11.7 cm; position of fins; number of fin lepidotrichia; presence of long pleural ribs; morphology of the axial support for the caudal fin; and scale morphology. Note that the outermost dorsal and ventral scale rows of the partial adult suggest its approximate body outline. A tiny partial *D. newarki* skeleton in front of and slightly overlapping the adult anal fin is recognized as an immature juvenile by: crude body length estimate of 1.7 cm and its tri-lobed caudalis with characteristic 12 - 13 lepidotrichia on each of the upper and lowerlobes. No scales and only indistinct suggestions of anterior portions of the juvenile are preserved. Also present are conchostracans (*Cyzicus* sp.), a large fish tail fragment and an isolated supplementary caudal fragment.

Orientations of the scattered conchostracans and of the large tail fragment at the bottom of the Fig. 1 photograph suggest the positions of the adult and juvenile *D. newarki* are not the result of prevailing currents. The apparent lack of sediment separating overlapping portions of the juvenile tail and adult anal fin (Fig. 2 photograph) indicates simultaneous burial of the adult and juvenile specimens.





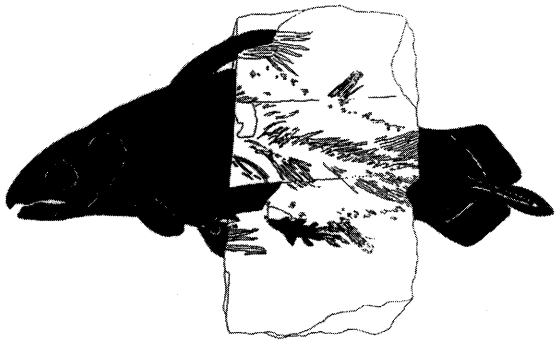


Figure 1. Clockwise from left, photograph, key sketch, and orientation sketch of NJSM 16697. The key sketch depicts important parts of the two specimens of interest on NJSM 16697, including the outermost dorsal and ventral scale rows of the partial adult to approximate its body outline. The orientation sketch uses silhouettes of missing portions of these two specimens to orient the partial remains with respect to the whole animals and indicate relative size.

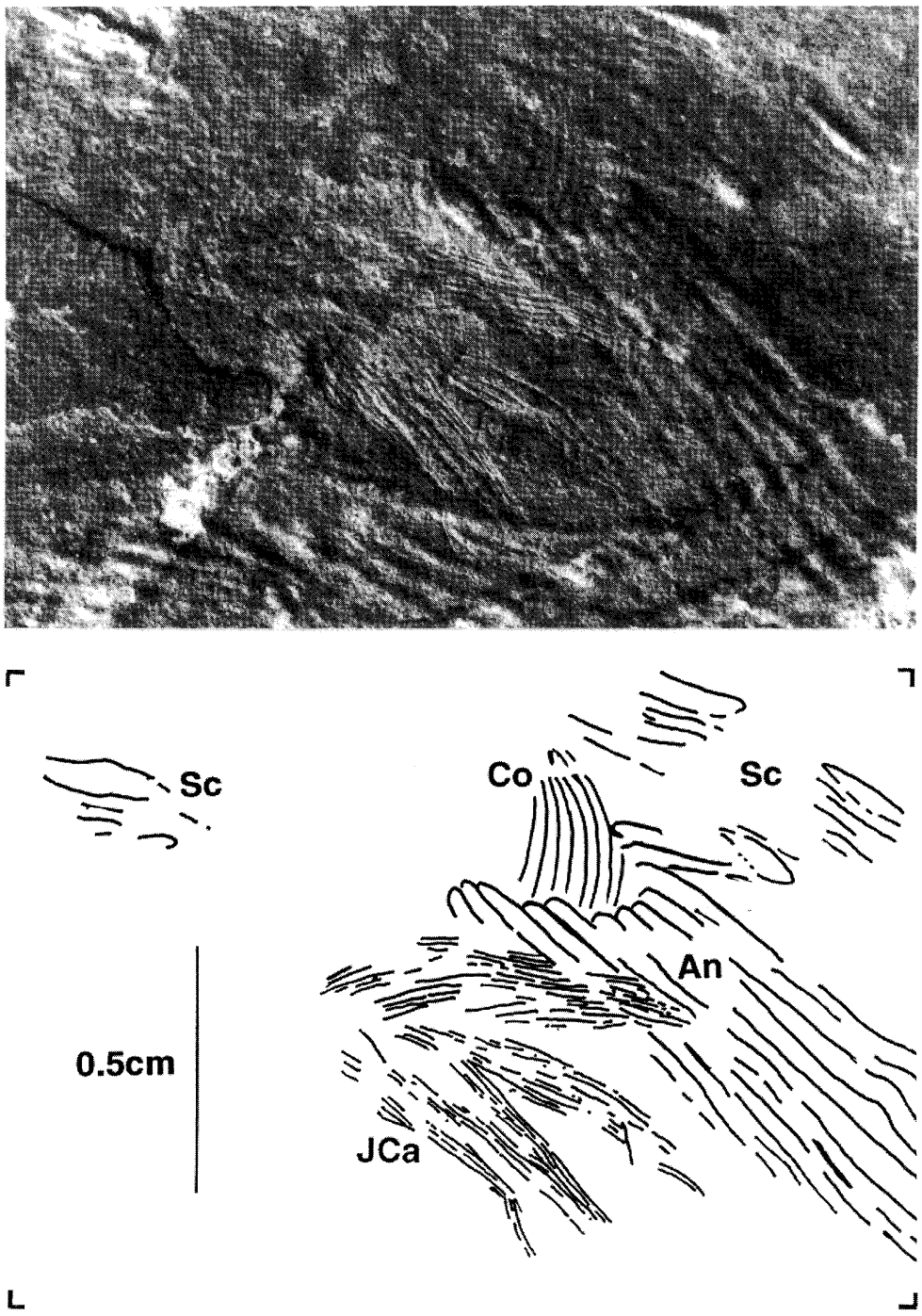


Figure 2. Photograph (top) and key sketch (bottom) detailing the juvenile *D. newarki* caudalis and the area surrounding it on NJSM 16697.

Comparative Evidence of Viviparity in Extant and Extinct Coelacanths

The extant coelacanth is viviparous

Data on reproduction in extant coelacanths has direct bearing on interpretations of the evidence relating to fossil coelacanth reproduction. A comparison of available data in extant and extinct coelacanths is detailed in Table 1. Over 170 captured specimens reveal *Latimeria chalumnae*, the only known extant coelacanth species, to be viviparous, lecithotropic and variably fecund (Smith et al., 1975; Thomson, 1991; Fricke and Frahm, 1992). Females containing 19-59 exceptionally large (8.5-9.0 cm) ovulated, unfertilized eggs and two gravid females

containing 5-26 advanced young (0.17-0.20 X adult body length) have been described (Smith et al., 1975; Thomson, 1991; Fricke and Frahm, 1992). A single oviduct is functional, with birth apparently occurring tail first at an estimated embryo length of 34-35 cm after substantial external yolk reserves have been resorbed (Smith et al., 1975; Thomson, 1991; Fricke and Frahm, 1992).

Previously reported evidence suggesting viviparity in extinct coelacanths

Comparison of known *Latimeria* specimens with earlier fossil evidence (Table 1) suggests an evolutionary conservatism in coelacanth reproduction. Schultze (1972) described yolk-sac young and an adult of the fossil coelacanth *Rhabdoderma exiguum* from the Middle Pennsylvanian. Reported body lengths suggest *R. exiguum* yolk-sac and yolk-sac resorbing young range 0.18-0.26 X adult length. Although Schultze (1972) interpreted these isolated, exceptionally large, yolk-sac young as supporting oviparity, it has been suggested they are embryos shed from stressed females and thus evidence of viviparity (Thomson, 1991). Watson (1927) described two small, incompletely ossified but completely articulated skeletons of the Jurassic coelacanth *Undina (Holophagus) penicillata* lying one above the other and facing caudally in the pelvic region of a much larger specimen of the species. Watson interpreted the smaller internal specimens as embryos rather than evidence of cannibalism. Embryo size suggests this species retained young within the oviduct to at least 0.18 X adult length. Comparison of embryo position in *Undina* (Watson, 1927) with that in *Latimeria* (Smith et al., 1975) suggests the fossil condition is compatible with the mechanism of oviductal development in extant coelacanths.

Evidence suggesting viviparity in the extinct coelacanth *D. newarki*

The new Lockatong Formation *D. newarki* specimens are illustrated in Figs. 1 and 2. The relevant material on NJSM 16697 consists of 1) a 4 cm long articulated adult midsection and 2) a closely associated partial *D. newarki* juvenile. The sex of the partial adult is undeterminable from skeletal characteristics as there is no indication that sexual dimorphism is evident in *D. newarki* (Schaeffer, 1952) and marked sexual differences in pelvic and anal fins do not occur in *Latimeria* (Thomson, 1991) or *Undina* (Watson, 1927). However, the juvenile's relative size, about 0.15 X adult length, and position, lying near to and with tail directed caudally from the presumed position of the adult's urogenital orifice, roughly match expectations for a mother and its expelled embryo which result from projecting knowledge of *Latimeria* reproduction to a species the size of *D. newarki.*

Table 1. Evidence supporting evolutionary conservatism in coelacanth reproductive mechanisms. [1] From Smith et al. (1975), [2] from Fricke and Frahm (1992), [3] from Watson (1927) and [4] from Schultze (1972). [*] Estimate based on Watson (1927) pl. 1 photograph and proportions of a reconstruction in Thomson (1991: fig. 3). [†] The style of preservation is unsuitable for a determination. [‡] Estimates based on incomplete adult and juvenile skeletons on NJSM 16697. [§] Large yolk sacs on 3.6-4.8cm young and resorbing yolk sacs on 4.5-5.3cm young.

Species	Age	Adult length (cm)	Length of young (cm)	Number of young	Location of young	External yolk sac
Latimeria chalumnae [1]	extant	160	30.1-32.7	5	oviduct	large
Latimeria chalumnae [2]	extant	179	30.8-35.8	26	oviduct	little to none
Undina penicillata [3]	Late Jurassic	34[*]	6.0	2	oviduct	?[†]
Diplurus newarki	Late Triassic	11.7[‡]	1.7[‡]	1	external, near urogenital opening	?[†]
Rhabdoderma exiguum [4]	Middle Pennsylvanian	20.2	3.6-5.3	?[†]	isolated specimens	large to resorbing[§]

Discussion

Evidence concerning reproduction in *Latimeria, Undina,* and *Rhabdoderma*, spanning 300 million years and a nearly 10 fold range in adult body size, suggests that a hypothesis of live birth in a Triassic coelacanth based on proportionate scaling of reproductive biology in a larger extant species is more than speculation. Live birth, evidence of which is rarely reported in fossil fish, is widespread in extant species (at least 420 chondrosteans and 510 teleosts, Wourms, 1981) and would be

an important finding in fossil coelacanths. Advantages and developmental constraints of viviparity, in concert with feeding and locomotory adaptations in all known coelacanths, could help explain the extraordinary anatomical conservatism and extreme longevity of this group of fishes. The new Lockatong Formation *D. newarki* specimens apparently preserve the expulsion of a developing young from the birth canal. This provides an additional datum supporting the hypothesis of *Latimeria* - like viviparity in extinct coelacanths.

Abundant *D. newarki* on Newark Basin Lockatong Formation slabs are housed in the collection of the American Museum of Natural History and the Princeton University Geology Museum collection, now at Yale Peabody Museum. These collections provide a sizable free-swimming fossil coelacanth population in which to look for further evidence of, and possibly test predictions resulting from, the live birth hypothesis. Despite an extraordinary range of inter- and intraspecific variation in the reproductive biology of extant viviparous fishes (Wourms, 1981; Meffe and Snelson, 1989), the extreme evolutionary conservatism of coelacanths suggests *Latimeria* to be a useful model on which to base predictions concerning the population age structure and allometric growth style of a viviparous *D. newarki*. There may be enough specimens of *D. newarki* to perform statistical analyses of population structure and the allometry of growth. It may even be possible to relate development and population data directly to age in *D. newarki*, since growth lines are present on the scales and some bones of *Latimeria* (Thomson, 1991) and Schaeffer (1952) describes well defined "annuli" on the scales of *D. newarki*.

Finding comparable styles of development and population structure in *D. newarki* and *Latimeria* would not prove the presence of viviparity in *D. newarki*, nor would their absence be incompatible with piscine viviparity per se. However, the absence of appropriate development style and/or suitably agestructured populations would be incompatible with a *Latimeria*-like viviparous reproduction. Also, studies of growth allometry in *D. newarki* could provide further evidence relating to the level of maturity of the presumed adult on NJSM 16697. Thus independent tests of the present hypothesis may be possible in this species. When added to the evidence from *Latimeria, Undina,* and *Rhabdoderma*, appropriate styles of development and population structure would provide strong independent support for live birth rather than an interpretation of a chance association of the new upper Triassic Lockatong formation specimens.

Conclusion

The unique situation of *D. newarki*, including a fossil specimen suggestive of viviparity, a living relative to serve as a plausible predictive model, and a sizable fossil population sample preserved in museum collections, will allow further examination of the hypothesis that live birth of precocial young is phylogenetically widespread in fossil coelacanths.

Acknowledgments

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References

Colbert, E.H. 1965. A phytosaur from North Bergen, New Jersey. *American Museum Novitates* 2230: 1-25.

Fricke, H. and J. Frahm. 1992. Evidence for lecithotrophic viviparity in the living coelacanth. *Naturwissenschaften* 79: 476-479.

Meffe, G.K. and F.F. Snelson, Jr. (eds.). 1989. *Ecology and Evolution of Livebearing Fishes (Poeciliidae).* Prentice Hall, Englewood Cliffs, NJ, 453 pp.

Olsen, P.E. 1980. Fossil great lakes of the Newark Supergroup in New Jersey; pp. 352-398 *in* W. Manspeizer (ed.), *Field Studies of New Jersey Geology and Guide to Field Trips*: 52 Annual Meeting of the New York State Geological Association. Newark College of Arts and Sciences, Rutgers University, Newark, NJ.

Olsen, P.E. 1991. Tectonic, climatic, and biotic modulation of lacustrine ecosystems - examples from Newark Supergroup of eastern North America; pp. 209-224 *in* B.J. Katz (ed.), Lacustrine Basin Exploration - Case Studies and Modern Analogs. *Memoirs of the American Association of Petroleum Geologists* No. 50.

Olsen, P.E. and J.J. Flynn. 1989. Field guide to the vertebrate paleontology of Late Triassic Age rocks in the southwestern Newark Basin (Newark Supergroup, New Jersey and Pennsylvania). *The Mosasaur* 4: 1-43.

Schaeffer, B. 1952. The triassic coelacanth fish *Diplurus* , with observations on the evolution of the Coelacanthini. *Bulletin of the American Museum of Natural History* 99(2): 25-78.

Schultze, H.-P. 1972. Early growth stages in coelacanth fishes. *Nature New Biology* 236: 90-91.

Smith, C.L., et al. 1975. *Latimeria*, the living coelacanth, is ovoviviparous. *Science* 190: 1105-1106.

Thomson, K.S. 1991. *Living Fossil: The Story of the Coelacanth.* W.W. Norton and Co., New York, 252 pp.

Watson, D.M.S. 1927. The reproduction of the coelacanth fish, *Undina. Proceedings of the Zoological Society of London* 1927: 453-457.

Wourms, J.P. 1981. Viviparity: the maternal-fetal relationship in fishes. *American Zoologist* 21: 473-515.